Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand

Richard P. Duncan, Robert J. Webster[1] and Carol A. Jensen[2]
Ecology and Entomology Group, Soil, Plant and Ecological Sciences Division, P.O. Box 84, Lincoln University, Canterbury, New Zealand (E-mail: duncanr@lincoln.ac.nz)
[1]Knight Frank (NZ) Ltd, P.O. Box 142, Christchurch, New Zealand
[2]20 Hyndhope Rd, Christchurch, New Zealand

Abstract: We studied vegetation change on 142 permanently marked transects spread throughout tussock grasslands of Otago and Canterbury, in areas subject to both pastoral and conservation management. The transects were established between 1982 and 1986 and re-measured between 1993 and 1999, providing a record of vegetation change at each site over an interval varying from 10 to 15 years. Each transect consisted of 50 quadrats, each 0.25m^2, in which the presence of all vascular plant species had been recorded. For each transect, we calculated the change between measurements in the mean number of species recorded per quadrat, and the change in the total number of species recorded per transect. Averaged across all transects, there was a significant decline in species richness between measurements at both the quadrat and transect scales. Small herbs (those ≤ 2 cm tall, excluding *Hieracium* species) showed the greatest decline. On average, more than one quarter of the small herb species present in a quadrat at the first measurement had disappeared within 10 years. Larger herbs, ferns, rushes, sedges and grasses (excluding *Chionochloa* species) also declined significantly in species richness, reflecting declines in the abundance of species in these groups. Woody species richness remained constant, while species in the genera *Chionochloa* and *Hieracium* increased significantly in mean quadrat species richness, reflecting increases in the abundance of these species along transects. The rate of decline in mean quadrat species richness was unrelated to, changes in the abundance of either *Chionochloa* or *Hieracium* species, or to an overall increase in total vegetation cover on transects. The rate of decline in species richness was also unrelated to the level of grazing or burning between measurements. However, the rate of decline in species richness was greater at lower elevation, on schist rock and on yellow-brown and yellow-grey soils. Our results suggest that a major compositional change is occurring in these' grasslands at a rate that is independent of local variation in management and independent of the widespread invasion of these grasslands by *Hieracium* species.

Keywords: grazing; plant invasion; species richness; tussock grassland; vegetation change.

Introduction

Since European arrival and the start of pastoral farming in the late 1800s, the high country tussock grasslands of South Island, New Zealand, have undergone major changes in vegetation structure and composition. In broad terms, this change has involved the replacement of tall tussock *(Chionochloa* species) grassland with short tussock *(Festuca novae-zelandiae)* grassland and subsequently a shift towards low-growing, exotic weed dominated communities or bare ground (Cockayne, 1919; Zotov, 1938; Connor, 1964, 1965; O'Connor, 1982). These vegetation changes have been attributed primarily to the impacts of pastoral farming, particularly the introduction of sheep, cattle and feral rabbits, and the increase in burning frequency associated with stock grazing. These impacts were most severe, and vegetation change was probably most rapid, during the early stages of European occupation of the high country. During this initial 'exploitation' phase stock numbers and burning frequency were high and tall tussock grasslands were rapidly converted to short tussock grasslands, particularly at relatively dry, low elevation sites (Zotov, 1938; Connor, 1964; O'Connor, 1982).

The 1950s marked a turning point in the management of tussock grasslands and heralded the beginning of the current era of 'range restoration' (O'Connor, 1981), with management policies aimed at reversing the changes in vegetation that were leading to extensive areas of degraded grassland dominated by exotic weeds. Pastoral farmers were provided with more secure land tenure and this, along with advances in technology and changes to the administration of the high country, encouraged investment in oversowing and fertilising of lower country, improved rabbit control, and reductions in the levels of stock grazing and burning in areas considered susceptible to those impacts (O'Connor, 1981; 1982).

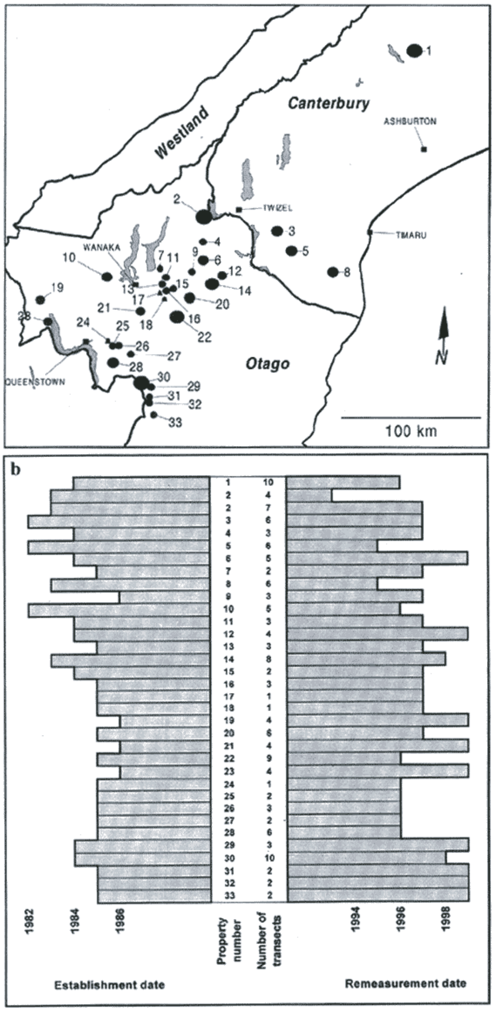

Figure 1. (a) Map of the study area showing the distribution of the 33 properties on which tussock grassland transects were sampled in Canterbury and Otago. The location of each property is indicated by a shaded circle, with the size of the circle proportional to the number of transects sampled on that property. (b) A list of the 33 properties showing the number of transects sampled per property and the years of the first and second measurement.

Despite these efforts, studies of vegetation change over the last four decades have revealed ongoing changes in the structure and composition of undeveloped tussock grasslands, generally towards increased dominance by exotic weeds and reductions in the diversity and abundance of native species (Scott *et al.,* 1988; Treskonova, 1991; Connor, 1992a; Rose *et al.,* 1995; Johnstone *et al.,* 1999). Some researchers have attributed these changes to the ongoing impacts of pastoral use. Treskonova (1991), for example, documented a marked decline in the diversity of native species, reductions in the cover of *Chionochloa* species, and an increase in the abundance of invasive *Hieracium* species from the mid 1960s to the late 1980s in the Mackenzie Basin. She inferred that this pattern of grassland degradation was the result of continued pastoral use. Other researchers have been more cautious about attributing changes in grassland composition directly to pastoral impacts, or have found little evidence for a causal link (Scott *et al.,* 1988; Connor, 1992a; Rose *et al.,* 1995). Consequently, there is uncertainty about the extent to which recent changes in tussock grassland vegetation have been driven primarily by recent pastoral impacts, and could therefore be managed by adjusting current pastoral use, or whether other processes are more important in driving vegetation change. Clearly, quantifying the patterns of vegetation change and determining their underlying causes is central to the long-term management of these tussock grasslands.

A network of permanent vegetation monitoring transects was established in the early 1980s by the former Department of Lands and Survey, primarily for investigating the effects of reducing livestock grazing on tussock grassland vegetation. These transects are spread throughout the central South Island on a wide range of land types managed for livestock grazing, or in areas transferred to the conservation estate where grazing has been excluded. Because they are located on sites subject to a range of pastoral impacts, these transects provide an opportunity to examine recent temporal changes in tussock grassland vegetation and to relate these changes to variation in management. 10 this study we report the results of a recent re-measurement of 142 of these transects, each providing a measure of vegetation change over a period of 10-15 years. We examine whether there has been any consistent change in vegetation composition over the last 10-15 years, and whether the nature of change differs on sites subject to different pastoral impacts during this period.

Methods

Transect location

We studied vegetation change on 142 permanently marked transects spread across the tussock grasslands of Otago and part of Canterbury (Fig. la). Along with their wide geographic spread, the transects occurred on sites sampling the range of environments associated with tussock grassland vegetation. The sites varied in elevation from 400 to 1890 metres above sea level, occurred on a range of soil and rock types, and encompassed vegetation types ranging from high altitude native tall tussock grassland to highly modified, lower altitude, exotic weed dominated communities and short tussock grasslands. The transects were established between 1982 and 1986 and were re-measured between 1993 and 1999, providing a record of vegetation change at each site over an interval varying from 10 to 15 years (Fig. 1b).

The transects are spatially clustered on 33 pastoral properties or conservation areas (collectively termed properties), with between I and II transects per property. One hundred and four of the transects were on pastoral lease land with stock grazing, although most of these were in blocks where stock grazing limits had been imposed. Thirty-eight transects were located in Crown Land Management Areas that had been completely retired from stock grazing prior to transect establishment, and are now under the control of the Department of Conservation. Within each property, transects were subjectively located at sites considered representative of the general vegetation of the area to be monitored. Although the 142 transects are not a random sample of tussock grassland sites throughout Canterbury and Otago, the management history of these sites has probably been similar to that over much of the South Island high country, with an early period of 'exploitative' pastoralism followed by relatively low levels of stock grazing during the current 'restoration era'.

Transect measurement and analysis of vegetation change

Each vegetation transect was 100 m long and marked at each end by a permanent fibreglass pole. Fifty quadrats, each 0.5 m by 0.5 m (0.25 m^2), were systematically located at two-metre intervals along each transect. Within each quadrat all vascular plant species rooted or overhanging the quadrat were recorded, and the total vegetation and litter cover in the quadrat was estimated visually in 5% classes. For each transect the following site factors were recorded: elevation, aspect, mapped soil type (brown-grey, yellow-grey or yellow-brown soils) and underlying rock type (schist or greywacke). A topographic relative moisture index (TRMI) was calculated (Parker, 1982) by summing values assigned to each transect with respect to: topographic position (gully, 20; basin, 15; fan, 15; face, 10; flat, 7; terrace, 7), slope configuration (concave, 10; convex, 0; linear, 5), slope steepness (< 3° = 10; 3-5.9° = 9; 6-8.9° = 8;...; ≥ 30° = 0) and slope aspect (scaled from 0 at 22.5° west of true north to 20 at 22.5° east of true south, through both east and west facing aspects). Transects were classed as being subject to one of three levels of grazing (high, medium or low-nil). Grazing by livestock, rabbits and any other feral animals was included in this assessment. Grazing classifications were based on informal grazing estimates provided by farmers or conservation area managers, along with field sign of grazing. Field sign included the presence of grazing animals in the area, evidence of browsing on vegetation, stock tracks and camps, and animal dung. Forty transects were classified as having experienced low to nil grazing, 80 as moderate and 22 as heavily grazed. The grazing level clearly reflected land tenure; 38 of the 40 transects classified as having low to nil grazing were on land managed by the Department of Conservation, while the remaining transects were on pastoral lease land. Transects were also classified according to whether they had been burnt in the interval between measurements (12 burnt, 130 unburnt).

In this paper we focus on overall changes in the abundance of species during the 10 to 15 year period between transect measurements as reflected in changes in the number of species recorded in quadrats and transects (i.e., changes in species richness). For each measurement, we calculated the mean number of species recorded per quadrat along each transect (mean quadrat species richness) and the total number of species recorded in each transect (transect species richness). We then calculated the change in species richness between measurements at each of these scales. Because measurement intervals differed, we converted each change in species richness to a rate per 10 yrs. A decline in mean quadrat species richness would reflect a net tendency for species to have decreased in quadrat occupancy along a transect (i.e., an overall decline in the local abundance of species), while an increase in mean quadrat species richness would reflect a tendency for species to have increased in local abundance, for new species to have colonised the transect, or both. A change in transect species richness would reflect a net gain or loss of species from the transect.

In addition to examining changes in mean quadrat and transect richness for all species, we examined changes in these measures for particular subsets of species, with subsets identified primarily on the basis of differences in growth form. Specifically, we examined the change in species richness for each of the following groups: grasses in the genus *Chionochloa,* other grasses, herb species in the genus *Hieracium,* other small herbs with vegetative parts usually ≤ 2 cm tall, other large herbs with vegetative parts usually > 2 cm tall, ferns, rushes/sedges, and woody species.

For each species, we determined whether the number of quadrats that a species occupied along each transect had increased, decreased or remained constant between measurements. We then identified those species whose quadrat occupancy had increased or decreased on more transects than expected using a binomial test, assuming increases or decreases occurred with equal probability.

Predictors of change in mean quadrat species richness

We identified factors associated with greater or lesser changes in mean quadrat species richness by fitting a mixed model to the data (Goldstein, 1995), with change in mean quadrat species richness as the response variable and the following site factors as covariates or fixed effects: elevation, TRMI, *Hieracium* response (classed as: no *Hieracium, Hieracium* stable or decreased, or *Hieracium* increased between measurements), *Chionochloa* response (classed as: no *Chionochloa, Chionochloa* stable or decreased, or *Chionochloa* increased between measurements), total vegetation cover (classed as: total vegetation cover stable or decreased, or total vegetation cover increased between measurements), grazing level, rock type, soil type (with brown-grey and yellow-grey soils in one category and yellow-brown soils in a second category) and burning history. For this analysis we excluded species in the genera *Chionochloa* and *Hieracium* from calculations of the change in mean quadrat species richness because changes in abundance of these species were included as factors in the model.

Transects in our data set were spatially clustered on properties (Fig. la) and are therefore unlikely to represent independent data points. The change in mean quadrat species richness for transects located on the same property will most likely be correlated because transects on the same property will share unmeasured features, including a similar history of past management and a similar environmental setting. To account for these property level correlates of change in mean quadrat richness, we included the categorical variable 'property' as a random effect in the mixed model (Goldstein, 1995). By doing this, we explicitly modelled the correlation among transects on the same property, ensuring that the resulting error terms were independent and therefore satisfied a basic assumption of the model. A further advantage of including 'property' as a random effect in the model is that inferences drawn from the model apply more generally to the larger population of properties in Canterbury and Otago and not just to the sample of properties included in this data set (Bennington and Thayne, 1994). The mixed model was fitted using the method of restricted maximum likelihood implemented in the procedure MIXED in SAS (SAS Institute, 1996). Model-corrected least-squares means for the categories of the fixed effects were obtained using the LSMEANS statement in procedure MIXED.

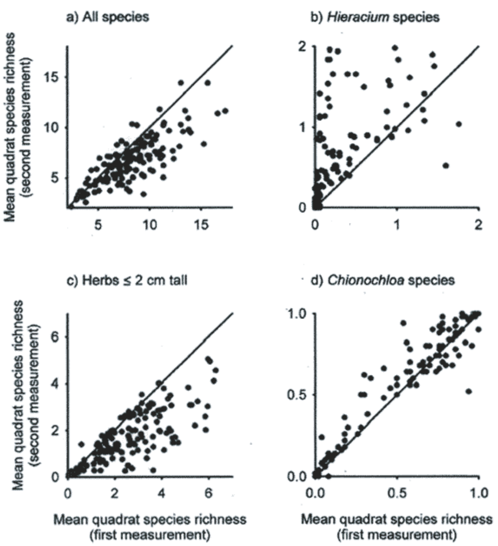

Figure 2. Mean quadrat species richness at the first measurement plotted against mean quadrat species richness at the second measurement for 142 tussock grassland transects in Canterbury and Otago. (a) for all species and (b-d) for three of the species groups listed in Table 1 Mean quadrat species richness has declined between measurements when transects fall below the line, and has increased between measurements when they fall above the line.

Results

Trends in mean quadrat species richness

Of the 142 transects, 118 had declined in mean quadrat species richness between measurements (Fig. 2). On average, the mean number of species recorded in the 0.25 m^2 quadrats along each transect declined by (mean ± SE) 1.25 ± 0.13 species (15.3%) per 10 yrs, a decline significantly less than 0 (*t-test*, t = 9.9, P < 0.001).

Species of different growth form exhibited different patterns within the overall decline in mean quadrat richness (Table 1, Fig. 2). Species in the genera *Hieracium* and *Chionochloa* increased significantly in mean quadrat richness, implying an overall increase in the number of quadrats that these species occupied along transects. The mean quadrat richness of woody species did not change significantly, while rushes/sedges, ferns, grasses (excluding *Chionochloa),* and small and large herbs all declined significantly in mean quadrat richness. The greatest decline was in small herbs; the mean quadrat richness of this group declined on average by 0.74 species (27.7%) per 10 yrs. In other words, in an average quadrat, more than one quarter of the small herb species present at the first measurement had disappeared 10 years later.

The mean quadrat richness of both annual and perennial species declined significantly but annual species had a disproportionately larger decline (Table 1). The

Table 1. Summary of the changes in mean quadrat species richness that occurred in 142 transects located in Canterbury and Otago tussock grasslands, by species groups. The t-value tests whether the change in mean quadrat species richness/10 yrs differs significantly from 0 (no change).

Species group	Mean quadrat richness at first measure	Change in mean quatrat richness/10 yrs	Std error of change	% change in mean quadrat richness/10 yrs	t-value (n = 42)
All species	8.21	-1.25	0.13	-15.3	9.9 ***
Hieracium species	0.25	+0.21	0.03	+84.2	7.2 ***
Chionochloa species	0.47	+0.02	0.01	+4.6	3.5 ***
Woody species	0.44	+0.01	0.01	+2.0	0.7
Grass species	2.18	-0.34	0.04	-15.7	7.9 ***
Herb (> 2 cm tall) species	1.60	-0.27	0.04	-17.1	6.7 ***
Fern species	0.05	-0.01	0.003	-19.2	3.2 **
Rush/sedge species	0.56	-0.13	0.02	-23.7	8.7 ***
Herb (□2 cm tall) species	2.68	-0.74	0.06	-27.7	11.4 ***
Annual species	1.00	-0.32	0.06	-31.8	5.1 ***
Perennial species	7.20	-0.93	0.10	-13.0	9.6 ***
Native species	6.15	-1.08	0.09	-17.6	11.5 ***
Introduced species (excluding *Hieracium)*	1.80	-0.38	0.07	-21.1	5.3 ***

** $P < 0.01$; *** $P < 0.001$.

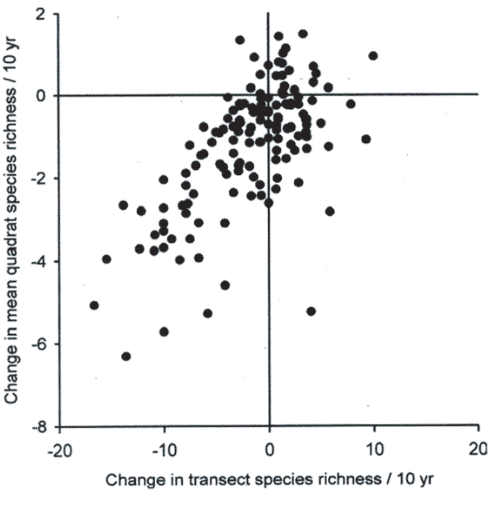

Figure 3. The relationship between change in mean quadrat species richness/10 yrs and change in transect species richness/10 yrs for 142 tussock grassland transects in Canterbury and Otago.

mean quadrat richness of both native and introduced species (excluding *Hieracium)* also declined significantly but in similar proportion.

The mean vegetation and litter cover in quadrats along each transect increased on 102 transects and remained stable or decreased on 40 transects. The average increase in vegetation and litter cover was (mean ± SE) 4.2% ± 0.64, an increase significantly greater than 0 (t-test, t= 6.6, $P < 0.001$).

Trends in individual species

Appendix 1 lists those species that either increased or decreased their quadrat occupancy on significantly more transects than expected. This reinforces several points evident in Table 1. First, many more species decreased in quadrat occupancy on an unusually large number of transects than increased, driving the overall decline in mean quadrat species richness. Second, the list of increasing species included *Chionochloa, Hieracium* and woody shrub species, while most species on the decreasing list were small herbs and grasses.

Trends in transect species richness

Change in species richness at the transect and quadrat scale was correlated (Fig. 3; r= 0.65, n = 142, $P < 0.001$) such that a large decline in mean quadrat species richness was generally matched by a large decline in transect species richness. Nevertheless, a larger proportion of transects showed a decline in mean quadrat richness (83%) than in transect richness (56%). Across all 142 transects, transect richness declined by an average of (mean ± SE) 1.83 ± 0.42 species (5.5%) per 10 yrs, a decline significantly less than 0 (t-test, t= 4.3, $P < 0.001$).

Most of the differences between growth forms in change in mean quadrat richness were repeated at the

Table 2. Mean change in mean quadrat species richness/10 yrs for transects differing in categories of the fixed effects. The means shown are least-squares, model-adjusted means, having adjusted for the other fixed effects, covariates (elevation and TRMI) and the random effect 'property' in a mixed-model. The type 3 *F*-values (and associated *P*-values) test whether the mean change in mean quadrat species richness differs for different levels of each fixed effect. Also shown are the type 3 F-values testing for a linear relationship between change in mean quadrat species richness and the covariates elevation and TRMI.

Variable	df[1]	Effect category	*n*[2]	Model-adjusted mean	Type 3 *F*	*P*
Elevation	1		142		11.54	< 0.001
TRMI	1		142		1.72	0.19
Hieracium response	2	None	30	-1.43	1.63	0.20
		Stable or decreased	13	-2.29		
		Increased	99	-1.81		
Chionochloa response	2	None	34	-1.59	1".47	0.24
		Stable or decreased	44	-1.81		
		Increased	64	-2.14		
Total vegetation cover	1	Stable or decreased	40	-1.81	0.08	0.78
		Increased	102	-1.88		
Grazing level	2	Low-nil	40	-2.13	0.38	0.69
		Moderate	80	-1.80		
		Heavy	22	-1.61		
Rock type	1	Greywacke	67	-1.32	8.23	< 0.01
		Schist	75	-2.37		
Soil type	2	BGE, YGE	28	-2.32	4.36	0.04
		YBE	114	-1.37		
Burning history	1	Burnt	12	-2.00	0.31	0.58
		Unburnt	130	-1.69		

[1]Degrees of freedom associated with each variable.
[2]Number of transects in each category.

transect scale (results not shown). There was a significant increase in the transect richness of *Hieracium* species and a significant decline in small herbs and grasses. While *Chionochloa* richness increased significantly at the quadrat scale, reflecting an increase in local abundance along transects, there was no significant increase at the transect scale, suggesting no net colonisation of new sites.

Predictors of change in mean quadrat species richness

Three factors were significantly associated with the amount of change in mean quadrat species richness (Table 2). Transects at lower elevation showed a greater decline in mean quadrat species richness, as did transects on schist rock and brown-grey or yellow-grey soils compared with transects on greywacke rock and on yellow-brown soils.

Discussion

On most of the 142 transects included in this study, plant species richness has declined at both the quadrat and transect scale during the 10-15 years between measurements. This overall decline in species richness is due to declines in abundance of many tussock grassland species over this period.

Some groups of species, however, increased in local abundance. Species of *Chionochloa* increased significantly in quadrat occupancy along transects but not in the total number of transects occupied, implying an increase in local abundance at previously occupied sites but no spread to new sites (*Chionochloa* colonised only one new transect and became extinct on two others between measurements). The increase in local abundance of *Chionochloa* is probably a response to the generally more conservative grazing and burning management over at least the last decade, relative to earlier periods. Indeed, level of grazing is the only variable that significantly predicts the change in *Chionochloa* quadrat occupancy (Type 3 $F = 7.62$, $P = 0.001$) when elevation, TRMI, *Hieracium* response, grazing level, rock type, soil type and burning history are included in a mixed model with 'property" as a random effect. (This analysis was restricted to the 107 transects on which *Chionochloa* was recorded initially.) As we would predict if the overall increase in *Chionochloa* was a response to more conservative grazing, *Chionochloa* abundance decreased on average at sites with a high level of grazing but showed an average increase at sites with medium and low-nil levels of grazing. Similar increases in *Chionochloa* abundance have been observed previously following reduced grazing (Rose and Platt, 1992; Lee *et al.*, 1993).

Species in the genus *Hieracium* increased significantly in both quadrat occupancy along transects and in the number of transects they occupied, results that concur with the well documented increase in local abundance and spread of *Hieracium* species throughout tussock grasslands in recent decades (Scott, 1984; Treskonova, 1991; Connor, 1992b; Scott, 1993; Rose *et al.,* 1995; Duncan *et al.,* 1997; Rose *etal.* , 1998; Johnstone et *al.,* 1999). *Hieracium* increase documented in this study resulted primarily from increases in abundance and spread of *Hieracium pilosella* and *H. lepidulum*.

In contrast, most other native and introduced species have declined in abundance in these grassland transects, leading to a significant and geographically widespread decline in species richness. The species that have declined the most are small herbs, followed by rushes/sedges, ferns, large herbs and grasses (excluding *Chionochloa* species). Other studies have also documented declines in the abundance of grassland species in parts of Canterbury and Otago during the last four decades. Treskonova (1991) reported a marked reduction in the number of native species recorded in 53 releves in the Mackenzie Basin of South Canterbury between the early 1960s and 1989. Connor (l992a) enlarged this data set and documented the loss or reduction in cover of many perennial grasses, rosette, mat and woody plants, of both native and exotic species. Rose et *al*. (1995) documented vegetation change on 27 transects in the Harper-Avoca catchment of Canterbury between 1965 and 1990. While they found no overall decline in species richness at the transect scale, they listed 15 species that had decreased significantly in abundance and only five species that had increased significantly. Thirteen of the 15 significantly decreasing species recorded in Rose *et al*. (1995) also decreased significantly in this study. Of the five significantly increasing species, three were in the genus *Hieracium*. Taken together, these results suggest that over recent decades and across large areas of the South Island high country many species have declined in abundance leading to a widespread local decline in the species richness of these tussock grasslands.

Explanations for the observed decline in species richness

We consider three explanations that could underlie the overall decline in species richness we have documented; these include sampling artefacts, increases in abundance of competitive dominants, and continued or heavy pastoral use.

Sampling artefacts

At least four kinds of sampling artefact could generate the patterns we observed. First, an artefactual decline in species richness could occur if the people who measured the transects the second time were not as competent at recognising or identifying species as those who measured the transects the first time, and so failed to record species that were actually present. In this study, one of us (C.A.J.) supervised and measured most transects on both occasions, ensuring that species identifications were accurate and consistent. Indeed, the decline in abundance of many species was noted in the field when the transects were being re-measured (the results from the first measurements were carried by field observers), and consequently particular attention was paid to ensuring that species were not overlooked during the second measurement. If anything, this would result in an underestimate of the magnitude of the decline in species richness.

Second, because we report the results of only two measurements for each transect, it is possible that the decline in species richness is just a short-term trend, reflecting climatic fluctuation from which the transects will recover. A short-term decline in species richness could have occurred, for example, if there had been a severe drought in the year prior to transect re-measurement. Any recovery of species richness after the drought would have been missed. We consider this sampling artefact unlikely because the initial and subsequent measurements of our transects were not all done in the same two years (Fig. 1b). Because transects show a similar decline in species richness regardless of years in which they were measured, short-term (i.e. year to year) fluctuations in climate are unlikely to explain the overall decline.

Furthermore, six transects located on one of the properties in this study were actually measured five times between 1982 and 1997, and annual rainfall data are available from this property for the period 1984-1992. The predominant pattern for these transects is one of decline in mean quadrat species richness rather than short-term fluctuation (Fig. 4a). Of the 24 changes in species richness that occurred between measurement periods *on* the six transects, 18 changes involved a decline in species richness while only six involved an increase. Four transects do show a synchronous fluctuation in species richness, increasing between 1988-1991 and then declining to 1997, but this fluctuation shows no obvious relationship to variation in annual rainfall (Fig. 4b).

Third, from one to eleven transects were clustered on each property, with the properties spread throughout tussock grasslands of Otago and Canterbury (Fig. la). It is therefore possible that the average decline in species richness was driven by large declines on just one or a few properties, with most transects not showing that pattern. This was not the case: Most transects declined in species richness (Figs. 2, 3). To check further, we calculated the mean change in quadrat species richness per property (rather than per transect, as previously); the same overall decline in mean quadrat richness was evident across the 33 properties as across the 142 transects.

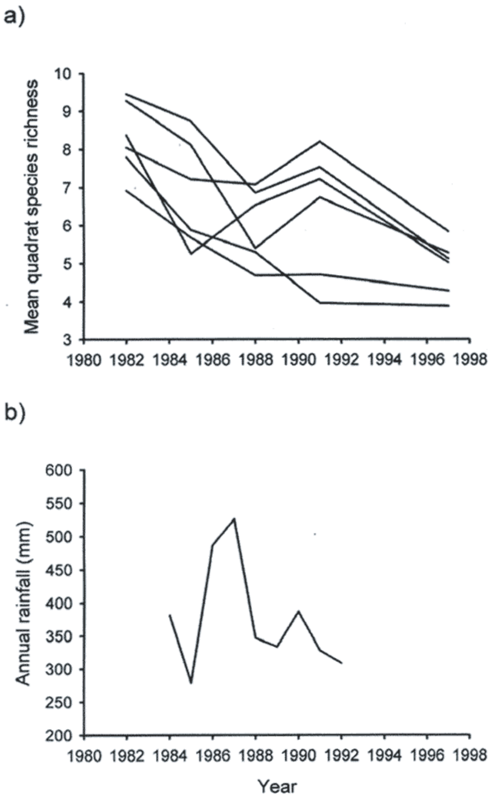

Figure 4. (a) The change in mean quadrat species richness from 1982-1997 for each of six transects on one of the properties in this study. Each transect was measured five times in this period: in 1982, 1985, 1988, 1991 and 1997. (b) Annual rainfall on the same property from 1984-1992.

Finally, the sites where transects were located in this study were not a random sample of tussock grassland sites in Canterbury and Otago. Many of the sites were chosen for sampling because they occurred in areas considered prone to grazing disturbance, areas where stock limits had been imposed. It is therefore possible that, while a decline in species richness was observed on these 142 transects, the transects are not representative of tussock grasslands in general and declining species richness is not a widespread feature in the South Island high country. We cannot discount this possibility. Nevertheless, as we have discussed, other studies have independently documented similar declines in species abundances or local species richness in these grasslands (Treskonova, 1991; Connor, 1992a; Rose *et al.,* 1995). Indeed, we are not aware of any study with reliable long-term records of compositional change in South Island tussock grasslands that has not documented a decline in the abundance of species similar to those recorded as declining in this study. The repeatability of these findings suggests that declining species richness has been a widespread feature of South Island tussock grasslands in recent decades.

Increases in the abundance of competitive dominants

Species richness is often low at sites where just one or a few species dominate because those species can monopolise essential resources and competitively exclude other species (Grime, 1973; Connell, 1978; Huston, 1994). We documented an increase in local abundance of *Chionochloa* and *Hieracium,* along with an increase in total vegetation cover on most transects. Hence, the decline in species richness could be driven by increases in local abundance of competitive dominants, such as *Chionochloa* and *Hieracium,* which locally exclude other species. This might explain why predominantly short statured and perhaps less-competitive species (Gaudet and Keddy, 1995), such as small herbs, rushes/sedges, grasses and annuals, show the greatest declines in species richness (Table 1).

If increases in abundance of competitive dominants are driving the overall decline in species richness, then we would expect the greatest declines to have occurred on those transects where the competitive dominants had increased the most. We would expect to see little or no decline in species richness on transects that either lacked competitive dominants, or on transects where abundance of competitive dominants remained stable. Our results do not support these predictions. For both *Chionochloa* and *Hieracium,* there was no significant difference in level of decline in mean quadrat richness among transects that lacked these species, transects in which abundance of these species remained stable or decreased, and transects in which abundance of these species increased between measurements (Table 2). More generally, an increase in abundance of competitive dominants should lead to an increase in total vegetation cover that in turn could lead to reduced species richness. Again, there is no evidence for this from our transects; the average decline in mean quadrat richness for transects on which total vegetation cover increased did not differ significantly from transects on which total vegetation cover remained constant or decreased (Table 2).

Continued or heavy pastoral use

Pastoral use, particularly livestock grazing, has been implicated as a cause of species declines in South Island tussock grasslands (Treskonova, 1991; Gibson and Bosch, 1996), although the mechanism by which grazing reduces species abundances and causes a decline in diversity has not been clearly articulated. In many grasslands, grazing serves to maintain high species diversity (Gibson *et al.,* 1987; Lord, 1990). Nevertheless, our results do not support the hypothesis that the overall decline in species richness is a consequence of ongoing grazing impacts. If this were the case then we would expect sites that had little or no grazing following transect establishment to show little or no decline in species richness. In contrast, there was no significant difference in the level of decline among transects subject to different levels of grazing (Table 2). Sites managed for conservation purposes where stock were excluded (the majority of sites classed as low-nil grazing) showed a decline in species richness similar to that of grazed sites on pastoral lease land. Likewise, there was no significant difference in the decline in mean quadrat richness between transects that had been burnt and transects that remained unburnt between measurements (Table 2).

To further examine the effects of excluding livestock grazing on plant species richness, we analysed data we had collected from four fenced exclosure plots located between 960 and 1500 metres above sea level. Three of the four plots were on properties already included in the main study. Each exclosure plot comprised a pair of permanently marked transects, one inside the exclosure that was free from livestock grazing and one in the adjacent grassland outside the exclosure that was subject to grazing. The exclosure plots were established between 1989 and 1991 and re-measured in 1998, thus covering an interval of 7 to 9 years during the same period as the transect measurements reported in the main study. The exclosure transects were measured using the methods we have described and we calculated the change in mean quadrat and transect species richness as before.

While plots varied in the degree to which they lost or gained species, in three of the four paired transects the decline in mean quadrat species richness was greater in the ungrazed than the grazed transect (Table 3). Again, there was no evidence in these data of a link between the level of livestock grazing and the decline in species richness. Rose *et al*. (1995) likewise compared changes in vegetation composition on sites subject to different levels of stock grazing. They observed significant declines in abundance of several species but found that these declines occurred regardless of whether sites were still grazed or had been retired from grazing.

Table 3. The change in mean quadrat and transect species richness/10 yrs for four exclosure plots, each with a pair of transects, one grazed and one ungrazed.

Exclosure plot	Change in mean quadrat richness/10 yrs		Change in transect richness/10 yrs	
	grazed	ungrazed	grazed	ungrazed
1	+0.09	-0.51	0.0	-2.2
2	-1.93	-1.42	-3.3	0.0
3	-5.00	-8.58	-2.5	-7.5
4	-0.23	-1.40	+10.0	+10.0

Alternative explanations

We find little evidence to support any of the above three explanations. The abundance of many species is declining in the tussock grasslands of Canterbury and Otago, leading to a significant decline in local species richness. This decline is geographically widespread and occurring at a rate that is independent of changes in the abundance of species in two competitively dominant genera (*Chionochloa* and *Hieracium*), independent of changes in total vegetation cover, and independent of the grazing and burning history in the period between measurements.

Three factors, elevation, rock type and soil type, are significantly related to the level of change in mean quadrat species richness having adjusted for the effects of other confounding factors (Table 2). Hence, any explanation for the overall decline in species richness must explain: (1) why species richness is declining in these tussock grasslands in the first place, (2) why the decline is greatest at low elevation, on schist rock and on brown-grey and yellow-grey soils, and (3) why species of differing growth form differ in their response, with small herbs, rushes/sedges and annuals showing disproportionately greater declines, and *Chionochloa, Hieracium* and woody species tending to remain stable or increase in abundance.

That the decline in species richness appears to be geographically widespread suggests that the processes driving this change are operating over much of the landscape. There are relatively few processes that act over such large areas. One thing all sites share is an early history of 'exploitative' pastoralism, with high stock numbers and repeated burning, followed by the current period of 'range restoration' characterised by lower stock numbers, less burning, and pasture development at some sites. High species richness could have been a response to loss of vegetation cover in the early exploitation phase, with the subsequent decline in species richness a response to vegetation recovery following reductions in grazing and burning. But, as we have shown, our results are not consistent with this scenario. The greatest declines in species richness have not occurred at those sites where recent recovery has been greatest, at least in terms of increases in total vegetation cover or *Chionochloa* abundance. An alternative possibility is that the early management phase initiated other widespread environmental changes that are now driving the decline in species richness. This could include changes to soil properties resulting from livestock trampling, vegetation removal and exposure of the soil surface, changes which have been shown to affect plant distributions elsewhere (Schlesinger *et al,* 1990). However, recent changes in soil properties through time, and in response to grazing removal, have not been particularly consistent or marked in South Island tussock grasslands (McIntosh *et al.,* 1994, 1996; Basher and Lynn, 1996). It is also possible that long-term climate change could have affected species distributions in recent decades. At best, however, we can only speculate on a role for these processes; our results currently provide little insight into the factors driving the broad compositional changes in these grasslands.

Implications

Regardless of the processes driving the overall decline in species richness, our results have some important implications. Research into tussock grassland vegetation has focused largely on understanding how variation in management, especially levels of grazing and burning, affects the structure and composition of the vegetation. It is clear that altering levels of grazing or burning can substantially alter local vegetation composition (Mark, 1965, 1994; Scott and Covacevich, 1987; Allan *et al.,* 1992; Rose and Plan, 1992). Nevertheless, .our results show that widespread compositional change has occurred in these grasslands independent of recent grazing or burning history, suggesting that factors unrelated to current management also playa significant role in the dynamics of these grasslands. Our understanding of tussock grassland dynamics would be enhanced by broadening the research focus to emphasise factors other than management that might be driving compositional change.

Our results also call into question the results of a recent study (Gibson and Bosch, 1996) suggesting that changes in the abundance of certain 'indicator' species can be used to monitor pastoral impacts in tussock grasslands. Gibson and Bosch (1996) recorded the abundance of species at a range of sites subject to different levels of grazing and inferred from this the likely temporal changes in species abundances that would occur in response to changes in the level of grazing at anyone site. However, several of the species identified in that study as indicators of grazing level in Otago grasslands show a significant decline in abundance across the transects measured in the present study (Appendix 1, e.g., *Poa colensoi, Festuca novae-zelandiae, Anisotome flexuosa* and *Raoulia subsericea*). These species appear to be part of a widespread decline in species richness that is occurring independent of variation in pastoral use. We therefore urge caution in the use of these indicator species because changes in their abundance may be driven by factors other than changes in pastoral use.

Finally, our results highlight the value of establishing and maintaining a widespread network of permanently marked plots to monitor vegetation change. While several studies have documented declines (and increases) in the local abundance of tussock. grassland species (Scott *et al.,* 1988; Treskonova, 1991; Connor, 1992a; Rose *et al.,* 1995), without the geographically extensive monitoring reported in this study we would probably have little idea of the extent or magnitude of what appears to be a consistent compositional shift that is occurring in these grasslands. This information is central to evaluating the broad response of these grasslands to changes induced in the current management era, and to providing a broader framework for understanding local changes in grassland composition in response to variation in local management and invasion by exotic species. The monitoring programme described in this study ceased to be funded in September 1999.

Acknowledgements

Funding for this work was provided through the Department of Conservation under Contract No. 2079, the former Department of Lands and Survey and the Commissioner of Crown Lands. We would like to acknowledge the contribution of Di Carter throughout the re-measurement programme, the many people who helped with transect measurements and the landowners for access to the properties. Thanks also go to Alan Rose and a reviewer for helpful comments.

References

Allan, B.E.; O'Connor, K.F.; White, J.G.H. 1992. Grazing management of oversown tussock country. 2. Effects on botanical composition. *New Zealand Journal of Agricultural Research* 35: 7-19.

Basher, L.R.; Lynn, I.H. 1996. Soil changes associated with cessation of sheep grazing in the Canterbury high country. *New Zealand Journal of Ecology 20:* 179-189.

Bennington, C.C.; Thayne, W.V. 1994. Use and misuse' of mixed model analysis of variance in ecological studies. *Ecology* 75: 717-722.

Cockayne, L. 1919. An economic investigation of the montane tussock grasslands of New Zealand, III. Notes on the depletion of the grassland. *New Zealand Journal of Agriculture* 19: 129-138.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Connor, H.E. 1964. Tussock grassland communities in the Mackenzie Country, South Canterbury ,New Zealand. *New Zealand Journal of Botany* 2: 325-351.

Connor, H.E. 1965. Tussock grasslands in the middle Rakaia Valley, Canterbury, New Zealand. *New Zealand Journal of Botany* 3: 261-276.

Connor, H.E. I 992a. The botany of change in tussock grasslands in the Mackenzie Country, South Canterbury, New Zealand. *Tussock Grasslands and Mountain Lands Institute Review* 49: 1-31.

Connor, H.E. 1992b. Hawkweeds, *Hieracium* spp., in tussock grasslands of Canterbury, New Zealand in the 196Os. *New Zealand Journal of Botany 30:* 247-261.

Duncan, RP.; Colhoun, K.M.; Foran, B.D. 1.997. The distribution and abundance of *Hieracium* species (hawkweeds) in the dry grasslands of Canterbury and Otago. *New Zealand Journal of Ecology* 21: 51-62.

Gaudet, C.L; Keddy,P.A. 1995. Competitive performance and species distribution in shoreline plant communities: A comparative approach. *Ecology* 76: 280-291.

Gibson, C.W.O.; Watt, T.A.; Brown, V.K. 1987. The use of sheep grazing to recreate species-rich grassland from abandoned arable land. *Biological Conservation* 42: 165-183.

Gibson, RS.; Bosch, O.J.H. 1996. Indicator species for the interpretation of vegetation condition in the St Bathans area, Central Otago, New Zealand. *New Zealand Journal of Ecology 20:* 163-172.

Goldstein, H. 1995. *Multilevel statistical models*. Edward Arnold, London, U.K.

Grime, J.P. 1973. Control of species density in Herbaceous vegetation. *Journal of Environmental Management* 1: 151-167.

Huston, M.A. 1994. *Biological diversity*. Cambridge University Press, Cambridge, U.K.

Johnstone, P.O.; Wilson, J.B.; Bremner, A.G. 1999. Change in *Hieracium* populations in Eastern Otago over the period 1982-1992. *New Zealand Journal of Ecology* 23: 31-38.

Lee, W.G.; Fenner, M.; Duncan, R.P. 1993. Pattern of natural regeneration of narrow-leaved snow tussock *(Chionoc;hloa rigida* ssp. *rigida)* in Central Otago, New Zealand. *New Zealand Journal of Botany* 31: 117-125.

Lord, J .M. 1990. The maintenance of *Poa cita* grassland by grazing. *New Zealand Journal of Ecology* 13: 43-49.

Mark, A.F. 1965. Effects of management factors on narrow-leaved snow tussock, *Chionochloa rigida*. *New Zealand Journal of Botany* 3: 300-319.

Mark, A.F. 1994. Effects of burning and grazing on sustainable utilisation of upland snow tussock *(Chionochloa* spp.) rangelands for pastoralism in South Island, New Zealand. *Australian Journal of Botany* 42: 149-161.

McIntosh,P.D.;Allen,RB.;Patterson,RG.I994.Tempora l changes of vegetation and soil carbon, nitrogen and pH on seasonally dry high country, South Island, New Zealand. *Rangeland Journal* 16: 3-15.

McIntosh, P.O.; Ogle, G.I.; Patterson, R; Aubrey, B.; Morris, J.; Giddens, K. 1996. Changes of surface soil nutrients and sustainability of pastoralism on grazed hilly and steep land, South Island, New Zealand. *Journal of Range Management* 49: 361-367.

O'Connor, K.F. 1981. Changes in the tussock grasslands and mountain lands. *Tussock Grasslands and Mountain Lands Institute Review 40:* 47-63.

O'Connor, K.F. 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology* 5: 97-107.

Parker, AJ. 1982. The topographic relative moisture index: An approach to soil-moisture assessment in mountain terrain. *Physical Geography* 3: 160-168.

Rose, A.B.; Basher, LR; Wiser, S.K.; Platt, K.H.; Lynn, I.H. 1998. Fac.tors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. *New Zealand Journal of Ecology* 22: 121-140.

Rose, A.B.; Platt, K.H. 1992. Snow tussock *(Chionochloa)* population responses to removal of sheep and European hares, Canterbury, New Zealand. *New Zealand Journal of Botany 30:* 373-382.

Rose, A.B.; Platt, K.H.; Frampton, C. 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: Effects of sheep grazing and exotic invasion. *New Zealand Journal of Ecology* 19: 163-174.

SAS Institute. 1996. *SAS/STAT software: Changes and enhancements for release* 6.12. SAS Institute, Cary, North Carolina, U.S.A.

Schlesinger, W.H.; Reynolds, J.F.; Cunningham, G.L.; Huenneke, LF.; Jarrell, W.M.; Virginia, R.A.; Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1048.

Scott, D. 1984. Hawkweeds in run country. *Tussock Grasslands and Mountain Lands Institute Review* 42: 33-48.

Scott, D. 1993. Time segment analysis of permanent quadrat data: Changes in *Hieracium* cover in the Waimakariri in 35 years. *New Zealand Journal of Ecology* 17: 53-57.

Scott, D.; Covacevich, N. 1987. Effects of fertilizer and grazing on a pasture species mixture in high country. *Proceedings of the New Zealand Grassland Association* 48: 93-98.

Scott, D.; Dick, R.D.; Hunter, G.G. 1988. Changes in the tussock grasslands in the central Waimakariri River basin, Canterbury, New Zealand. *New Zealand Journal of Botany* 26: 197-222.

Treskonova, M. 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, *New Zealand. New Zealand Journal of Ecology* 15: 65-78.

Zotov, V.D. 1938. Survey of the tussock-grasslands of the South Island, New Zealand. *New ZealandJournal of Science and Technology 20:* 212A-244A.

Appendix 1. Species whose quadrat occupancy increased or decreased on significantly more transects than expecte between measurements (tested using a binomial test assuming that increases or decreases were equally likely to have occurred).

Increase / decrease	Growth form	Species	A/P[1]	N/I[2]	Number of transects3			P [4]
					dec	con	inc	
Increase	Grass	*Chionochloa* species	P	N	21	23	64	***
		Anthoxanthum odoratum	P	I	23	5	58	***
	Hieracium	*Hieracium aurantiacum*	P	I			5	*
		Hieracium lepidulum	P	1	5	2	64	***
		Hieracium pilosella	P	1	7	2	84	***
		Hieracium praealtum	P	1	18	5	46	***
	Large herb	*Prasophyllum colensoi*	P	N	3		10	*
		Celmisia viscosa	P	N	2	1	9	*
		Taraxacum magellanicum	P	N			5	*
	Woody	*Carmichoelia petriei*	P	N	1		9	*
		Coprosma cheesmanii	P	N	1		9	**
		Discaria toumatou	P	N	5	4	25	***
		Dracophyllum muscoides	P	N	6	5	15	*
		Dracophyllum pronum	P	N	3	4	12	*
		Dracophyllum uniflorum	P	N	6	1	19	**
		Gaultheria depressa var. *novo*	P	N	22	7	39	*
	Rush/sedge	*Carex kirkii* var *kirkii*	P	N	4		13	*
Decrease	Grass	*Agrostis muelleriana*	P	N	33	5	12	**
		Agrostis petriei	P	N	27		5	***
		Aira caryophyllea	A	1	19	1	9	*
		Bromus hordeaceus	A	1	16		4	**
		Dactylis glomerata	P	1	23	1	8	**
		Dichelachne crinita	A	N	26	2	9	**
		Elymus solandri	A	N	45	4	14	***
		Festuca novae-zelandiae	P	N	58	8	34	**
		Koeleria cheesemani.i	A	N	23	1	3	***
		Lachnagrostis filiformis	A	N	20	3	10	*
		Poa cita	P	N	13		5	*
		Poa colensoi	P	N	104	8	24	***
		Poa lindsayi	A	N	28		8	***
		Vulpia bromoides	A	1	20		3	***
	Small herb	*Anaphalioides bellidioides*	P	N	29	8	6	***
		Arenaria serpyllifolia	A	1	17	1	5	**
		Brachyscome longiscapa	P	N	24	7	11	*
		Colobanthus strictus	P	N	16		1	***
		Dichondra repens	P	N	5	2		*
		Epilobium alsinoides	A	N	14		5	*
		Epilobium atriplicifolium	A	N	17		2	***
		Geranium microphyllum	P	N	19	2	6	**
		Geranium sessiliflorum	P	N	56	6	12	***
		Gnaphalium mackayi	P	N	21	2	10	*
		Hydrocotyle novae-zelandiae	P	N	44	2	8	***
		Hypochoeris radicata	P	1	77	10	23	***
		Lagenifera cuneata	P	N	28	4	9	**
		Leptinella pectinata	P	N	29	2	8	***
		Leptinella pectinata ssp. *villosa*	P	N	7			**
		Leptinella pusilla	P	N	6	1		*
		Leptinella serrulata	P	N	8		1	*
		LeucopogonfraSeri	P	N	47	10	29	*
		Myosotis pygmaea	P	N	8		1	*
		Ophioglossum coriaceum	P	N	17	1	1	***
		Oxalis exilis	P	N	14	I	3	**
		Phyllachne colensoi	P	N	9		2	*
		Plantago lanigera	P	N	22	2	5	***
		Ranunculus foliosus	P	N	21	2	7	**
		Raoulia australis	P	N	16		6	*
		Raoulia parkii	P	N	11	2	2	*

Appendix 1 cont.:

Increase / decrease	Growth form	Species	A/P[1]	N/I[2]	Number of transects[3] dec	con	inc	*P*[4]
Decrease (cont.)		*Raoulia subsericea*	P	N	62	7	36	**
		Rumex acetosella	P	I	94	7	24	***
		Scleranthus uniflorus	P	N	44	6	20	**
		Stellaria gracilenta	P	N	21	3	3	***
		Trifolium dubium	A	I	24	1	4	***
		Wahlenbergia albomarginata	P	N	88	6	17	***
		Wahlenbergia gracilis	P	N	8			**
	Large herb	*Acaena caesiiglauca*	P	N	39	4	15	***
		Aciphylla montana	P	N	5	1		*
		Anisotome flexuosa	P	N	39	5	21	*
		Brachyglottis haasrii	P	N	11	2	3	*
		Cerastium fontanum	P	1	40	1	14	***
		Crepis capillaris	A	1	43	2	24	*
		Helichrysum filicaule	P	N	25	5	10	**
		Taraxacum officinale	P	I	19		5	**
		Viola cunninghamii	P	N	91	5	13	***
		Vittadinia australis	P	N	13	1	5	*
	Rush/sedge	*Carex breviculmis*	P	N	28	1	8	***
		Luzula pumila	P	N	24	3	10	*
		Luzula rufa	P	N	84	8	19	***
	Woody	*Pimelea oreophila*	P	N	46	11	29	*
		Cover of vegetation and litter			35	5	102	***

[1]Classification of species as annual (A) or perennial (P).
[2]Classification of species as native (N) or introduced (I).
[3]The number of transects on which the number of quadrats occupied by a species decreased between measurements (dec), remained constant between measurements (con), and increased between measurements (inc).
[4] The P-value for the binomial test;* $P < 0.05$.** $P < 0.01$, *** $P < 0.001$.